



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

LOCOMOTION IN TWO SPECIES OF THE GASTROPOD GENUS *ALECTRION* WITH OBSERVATIONS ON THE BEHAVIOR OF PEDAL CILIA.

MANTON COPELAND,

SEARLES BIOLOGICAL LABORATORY, BOWDOIN COLLEGE.

INTRODUCTION.

In a paper on locomotion in gastropods Parker ('11) has pointed out that the mud snail, *Alectrion (Ilyanassa) obsoleta* Say, exhibits no rhythmic pedal movements such as are readily observed in most snails, and concludes that progression is accomplished by arrhythmic muscular activity. He writes: "The movement of the foot of *Ilyanassa* has a most striking resemblance to that of the foot of a planarian in which cilia may be the chief motor organs, but on testing the foot of *Ilyanassa* with carmine suspended in sea water, not the least evidence of cilia could be discovered." In subsequent accounts of gastropod locomotion *Alectrion obsoleta* has been cited as representing the only definitely known case of arrhythmic movement. Recently, however, Crozier ('19) has reported another example, that of *Conus agassizii* from Bermuda.

In the course of studies on the reactions of *Alectrion* I became interested in the locomotion of the animal and tested the foot for cilia by dropping carmine grains on its ventral surface. Much to my surprise the carmine was carried down the foot, and when the latter was examined under the microscope the under surface was found to be covered with cilia. Another related species, *Alectrion (Tritia) trivittata* Say, which showed no evidence of pedal waves likewise proved to have a ciliated foot.

That cilia occur on the feet of certain species of gastropods has been known for some time, but that they function as locomotor organs, however, has been questioned, and I believe that no detailed study of their behavior has been made. Olmsted ('17) has recently reported finding cilia on the feet of three species of marine snails from Bermuda, which showed no evidence of pedal

waves, and attributes their locomotion to ciliary action. Since, however, it is held that progression may be brought about by muscular activity without the appearance of pedal waves (arhythmic locomotion), the presence of cilia and the absence of waves does not signify necessarily that locomotion is accomplished by cilia. It is conceivable that pedal cilia have some other function, such as freeing the foot from foreign material or distributing mucus. If some such conception of ciliary function had not been held by students of gastropods, movement by ciliary action should have been recognized long ago as unquestionably constituting one type of locomotion in these animals. Walter in 1906 described the mechanism of locomotion in the pond snail, *Lymnæus elodes* Say, as consisting of "a complex muscular foot clothed on the ventral surface with cilia which act on a mucus track," and did not record finding any pedal waves, yet this case, as far as I know, has never been cited as substantiating the theory that gastropod locomotion may sometimes be effected by cilia.

In view of these facts it seemed desirable to investigate in some detail the behavior of the cilia on the feet of *Alectrion* in the hope of throwing light upon the possible relation between ciliary action and locomotion. The work was carried on at the Marine Biological Laboratory at Woods Hole, and I wish to express my gratitude to the director, Dr. Frank R. Lillie, for his kindness in granting me the facilities of the laboratory.

CILIARY BEHAVIOR.

Alectrion trivittata.—The foot of *Alectrion trivittata* in an individual of medium size measures 10 or 12 mm. in length by 4 or 5 mm. in width. The anterior end is truncated and auriculate. Back of the lateral, pointed processes the foot is narrowed somewhat before it expands and tapers toward the posterior end, which is bifurcated and bears two small tentacles. It is more slender than the foot of *Alectrion obsoleta* and considerably thinner, a feature which makes the species a favorable one for the study of ciliary activity under the microscope.

As soon as it was recognized that the under surface of the foot was ciliated the question arose: Were the cilia active during

locomotion, and if so, when the animal came to rest, did ciliary movement stop, or did it continue without effecting forward movement? That the cilia did not beat continuously was soon demonstrated. A support for the snail was made by fastening with "sticky-wax" a short glass tube to the bottom of a glass dish containing sea water. The snail's shell was then stuck upside down to the end of the pedestal so that the ventral surface of the foot when fully expanded was at the level of the water. In this position the animal usually exhibited righting movements for a time, but soon spread out its foot on the surface film of the water. Often the flicker of the cilia could be seen with the naked eye and readily observed under a hand lens. Grains of carmine were swept down the foot by ciliary activity. At other times, however, the cilia were quiescent and carmine grains remained on the foot where they were dropped. When a snail resting in this position was stimulated by touching one of its tentacles with a piece of fish meat, the proboscis was protruded and the cilia began beating. The proboscis was often worked over the surface of the foot and at that time the ciliary movement was greatly reduced or stopped. Usually after the proboscis was withdrawn the cilia showed vigorous activity, the foot was stretched out its full length, and the animal appeared as it did when moving upside down on the surface film of the water, a form of progression often exhibited when free in the aquarium. In the later situation its behavior was essentially like that when fixed in the position just described. As it moved along the surface of the water the cilia could be seen in motion and carmine grains were swept with the mucus down the foot. Frequently the proboscis was extended and moved about in various directions, and at this time ciliary activity and locomotion ceased.

By placing the dish, in which an inverted snail was fastened, on the stage of a microscope, and by using a low power objective the fringe of long cilia projecting from the anterior border of the foot could be clearly observed. In one instance when the animal was becoming quiet after feeding, the cilia could be seen beating slowly near the tip of one of the anterior lateral foot processes, whereas other cilia nearer the median position were

motionless. Moving cilia were observed slowing down and coming to rest, and passive ones becoming slightly active. Suddenly all the cilia under observation began to beat at high speed, when compared with the slower movement first recorded, and the foot process moved out of the field of vision. The snail was now showing its normal surface "swimming" activity.

The relation of ciliary movement to locomotion was finally studied by observing under the microscope snails which were moving on the under side of a glass slide placed across a dish full of sea water. A resting animal showed the cilia on the anterior border and ventral surface of the foot passive. Sometimes, when the snail was feeding, one of the lateral foot processes was moved or contracted slightly and some local beating of the cilia of short duration occurred. When the animal was moving, all the cilia which could be seen were active, and moreover, the rate at which they beat was distinctly correlated with the speed of locomotion. Rapidly beating cilia decreased their rate of movement and came to rest when the animal did, and became active again when locomotion began. Very satisfactory observations were made by placing the snails on the under surface of a slide, which had been smeared with fish meat, and allowing them to feed in this inverted position out of the water. Under these conditions they frequently progressed short distances and stopped, and the cilia in turn were seen to start beating, to continue slowly while the animal moved, and then to come to rest. When the rate of locomotion was increased, the cilia beat so rapidly that they could only with difficulty be seen at all.

A microscopic examination of the cilia of snails moving and floating at the surface of the water confirmed the observations already reported.

Alectrion obsoleta.—The foot of *Alectrion obsoleta* resembles that of *Alectrion trivittata* but is thicker, not so long in proportion to its width, rounded at the posterior end and lacks posterior tentacles. The behavior of the cilia were studied by some of the methods described in connection with the work on *Alectrion trivittata*, and the results obtained were so closely similar it is unnecessary to report them in detail. The thicker foot of the

mud snail made microscopic observation of the cilia on the ventral surface more difficult, but they could be seen when beating, and those along the anterior border were clearly visible at all times.

A comparison of the habits of the two species brought out one striking difference. Whereas *Alectrion trivittata* often floats or moves upside down at the surface of the water after the manner of certain fresh-water gastropods, *Alectrion obsoleta* was never observed to do so. Dimon ('05) in her monograph on the latter species states that young individuals may float on the surface but that the older ones very rarely do, and then only under unusual circumstances, and concludes that the shell of the adult is too heavy to permit it. It was impossible therefore to observe the behavior of the cilia on the foot of a freely floating mud snail.

The study of the two species of *Alectrion* shows unquestionably that beating cilia are characteristic of a moving snail, and that when the animal is at rest the cilia are motionless or exhibit only local activity. It is equally clear that the rate of ciliary movement is correlated with that of locomotion.

The reason why Parker, in the investigation referred to, failed to find cilia on the foot of *Alectrion obsoleta* was undoubtedly because when he placed carmine on them they happened to be quiescent. Only the unusual behavior of the cilia prevented their immediate discovery by the test he applied.

COMPARISON OF LOCOMOTOR WITH CILIARY RATES.

The foregoing observations are strongly in favor of the view that progression in *Alectrion* is accomplished by ciliary action. In order to test these conclusions further, the rate of locomotion was compared with the rate at which grains of carmine were driven over the surface of the foot by the beating cilia. The latter may be termed the ciliary rate. By the use of a stop-watch it was an easy matter to secure a series of records indicating the speed at which the snails traveled a distance of 5 mm. over the bottom of a glass dish containing sea water. In order to obtain a ciliary rate, the snail was fixed upside down on a support so that its foot when expanded was at the surface of the water.

A millimeter rule was fastened above the foot. Particles of dry carmine were then dropped on the water and as they were driven with the mucus down the foot by the active cilia, it was possible to record their speed over a distance of 5 mm. with considerable accuracy.

For some time all attempts at securing the ciliary rate for *Alectrion obsoleta* were unsuccessful. The snails either continued in their efforts to right themselves or else failed to expand their feet at the surface of the water, as *Alectrion trivittata* did with little hesitancy. When about to abandon the experiment some individuals not fully grown were tried, and their behavior was so satisfactory the desired records were readily obtained. In one instance continuous ciliary movement was watched for about three quarters of an hour. It is quite possible that the difficulty encountered with the older individuals was due to the fact that in the adult state the species does not have the habit of surface floating, whereas the younger animals adapted themselves to the inverted position more readily because they had more recently abandoned it under natural conditions.

The results of the tests made upon *Alectrion obsoleta* are shown in Table I. They indicate that the average locomotor rate is practically identical with the rate at which carmine grains are driven along the foot by the beating cilia.

TABLE I.
Alectrion obsoleta.

Locomotor Rate. (Rate at which Snails Moved a Distance of 5 Mm.).				Ciliary Rate. (Rate at which Carmine Grains were Carried a Distance of 5 Mm. Over Ciliated Foot.)	
Animal number	1	2	6 individuals	1	2
Number of trials	25	25	10 each	25	25
Average time in seconds	2.4	2.9	3.	2.5	3.

Animal number one proved to be a faster moving individual than any of the others timed, and it will be noted that the average ciliary rate is also fast. Considering the fact that the cilia are subject to great variation in rapidity of movement, the correspondence in rates is closer than might be expected, and to my mind affords conclusive evidence that locomotion is entirely dependent on the action of cilia.

Turning now to Table II it will be seen that the average rate of locomotion of *Alectrion trivittata* is twice as fast as that of the mud snail. If one watches for a moment the two species moving about in an aquarium, he does not require the use of a stopwatch to be convinced of this difference. The average ciliary rate of

TABLE II.
Alectrion trivittata.

<i>Locomotor Rate.</i> (Rate at which Snails Moved a Distance of 5 Mm.).				<i>Ciliary Rate.</i> (Rate at which Carmine Grains were Carried a Distance of 5 Mm. Over Ciliated Foot.)	
Animal number	1	2	6 individuals	1	2
Number of trials	10	10	10 each	10	10
Average time in seconds	1.8	1.3	1.5	2.7	2.1

Alectrion trivittata (2.3 seconds in eighty trials) is also faster than that of the mud snail, but slower than its own locomotor rate. The latter conclusion is based on many more trials than are recorded in the table. Does this mean that some arhythmic muscular operation is associated with ciliary movement and is responsible for the difference between the two rates, or do the cilia tend to beat faster when the snail is moving on its foot than they do when it is fastened on its back? An investigation of the locomotion of small pieces of the foot led me to believe that the latter explanation is the true one.

The behavior of the cilia on an excised foot will be described later in detail, and it is only necessary to record here that fragments of the foot a few millimeters long move at times rapidly over the substrate by ciliary action. The direction of their movements, however, was so uncertain it was necessary to time their speed over a distance of 2.5 mm. Some of these pedal fragments frequently moved at the rate of 5 mm. in 1.6 seconds and occasionally in 1.2 seconds, or faster than the average rate of locomotion recorded for six snails in Table II. In the case of these small pieces of the snail's foot there was no possibility that locomotion was in any direct way brought about by muscular movements. It was entirely the result of ciliary action, and the resultant speed was closely similar to the usual locomotor rate of the species. Under the microscope the cilia on the frag-

ments were sometimes seen at rest, again beating slowly and frequently at a high rate of speed, all accounting perfectly for the erratic movements of the fragments. There is no evidence that the locomotor mechanism of *Alectrion trivittata* contains any important factor not represented in that of *Alectrion obsoleta*, and I believe that progression in both species is accomplished by cilia.

If, as it appears, the rapidity of ciliary movement in *Alectrion trivittata* tends to be reduced when the animal is held with the ventral side of its foot at the surface of the water, some explanation of this peculiarity should be sought. I believe it is to be found in its habit of surface floating and moving, one not shared by adult mud snails. Observation of the snails' movements at the surface of the water gives one the immediate impression that this form of activity is a decidedly leisurely one associated with feeding. A snail may remain floating with extended proboscis for a long time, and when it moves, it is often for short distances in an apparently aimless way. At such times the cilia probably beat more slowly than they do when the animal is moving in a definite course over a substrate, as it was when the locomotor rates were taken.¹ When the snail is fixed to a support with its expanded foot at the surface of the water, its normal floating position is closely simulated. It accepts the inverted position often without showing any extended disturbance, and always exhibits the feeding reaction when stimulated with fish meat. It would not be surprising, therefore, if the behavior of the cilia were similar under these two conditions, and I believe that a somewhat reduced ciliary activity is characteristic of both.

CILIARY CONTROL.

In connection with the investigations described in the preceding pages there developed the exceedingly interesting problem of ciliary control. Doubtless it has occurred to the reader that the

¹ That snails move more slowly at the surface of the water than they do over a glass surface is perfectly clear, the average speed of locomotion in the former situation, based on thirty-four trials, being at the rate of 5 mm. in 2.7 seconds. Drawing conclusions, however, on the rapidity of ciliary movement by direct comparison of these two locomotor rates may not be justified, for a substrate is not present in both cases.

behavior of the pedal cilia of *Alectrion* suggests that they have in some way been appropriated by the nervous system and are controlled directly or indirectly by nervous impulses. Although little more than a beginning has been made in the study of this phase of the problem, the results of certain experiments are sufficiently important to warrant a preliminary report at this time. They have been obtained for the most part from a study of ciliary behavior after the foot has been removed from the rest of the snail's body.

When the somewhat contracted, excised foot of *Alectrion trivittata* is placed in sea water and viewed under a microscope the greater number of cilia are seen to be motionless. If now the anterior margin of the foot is watched, it will be observed that at intervals slight contractions of the border occur accompanied by the beating of the anterior fringe of cilia over the area moved. This muscular movement is not extensive, but consists of a sudden withdrawal of a short segment of the pedal border so that for a moment it appears slightly indented, the contraction being immediately followed by an expansion which restores the normal contour of the foot. The ciliary activity is also but a momentary affair and is restricted to the contracted region. The cilia usually appear to beat either synchronously with the contraction or directly after it, but in certain instances ciliary movement seems to precede slightly the muscular movement. These contractions accompanied by local ciliary action sometimes continue for hours. Sooner or later, however, the twitching of the muscles becomes more vigorous and frequent, and the cilia fail to come to rest between contractions. Some of them may be beating continuously at the same time that others are still showing intermittent activity associated with muscle movements. Finally the cilia are in motion, not only along the entire anterior border and lateral processes of the foot, but also over the ventral surface, and in the latter position contractions are also going on. At this time the anterior cilia exhibit great variation in rapidity of movement. Occasionally they slow down nearly coming to rest in the intervals between contractions, and at other times move so fast that not the slightest flicker can be seen, the ciliary fringe appearing like a broad

hyaline membrane. This high rate of movement is always associated with muscular contractions. Why it was that *Alectrion trivittata* sometimes moved so swiftly was never fully understood until I had witnessed in this way the possibilities of ciliary motion.

The third stage of ciliary activity is seen as a rule a number of hours later, often about twenty-four hours after the foot is severed from the body. At this time all muscular movement has ceased and the whole foot has become expanded. The cilia are beating everywhere at moderate speed, and if a given area is watched, no variation in the rapidity of movement is observed. The contrast between this uniform rate of ciliary movement and the preceding highly variable one is very striking. The cilia continue beating until maceration sets in and the epithelium begins to break down.

Having determined from a series of tests that the ciliary activities described above occurred with remarkable constancy, a means was sought of controlling muscular contractions without directly affecting the cilia. Previous experience had shown that magnesium sulphate is an excellent anæsthetic for marine gastropods and one that appears to leave no undesirable effects. It proved to be equally valuable in the study of ciliary behavior. When a foot of *Alectrion trivittata* in which muscular movements are going on is placed in a ten per cent. solution of magnesium sulphate made up in sea water, all contractions cease in a few minutes and the foot remains passive. The cilia, however, which are vigorously beating when muscular activity subsides, continue to do so for many hours with only gradually decreasing speed, whereas those which are quiescent remain so. Moreover, if there is initial variation in the rate of ciliary movement in different parts of the anterior border of the foot, it is maintained, and the cilia beating the fastest remain active the longest time; but changes in the speed of ciliary movement over a given area, which are so striking when the foot is in sea water and muscular contractions are in progress, never occur after contractility is inhibited by magnesium sulphate. It is also clear that those cilia which are moving most rapidly, or with the least interruption, when the foot is in sea water tend to beat the fastest when

the foot is removed to a solution of magnesium sulphate. If now the foot is returned to sea water, muscular contractions reappear in a few minutes and ciliary behavior is just the same as it was before the transfer.

These experiments indicate that the pedal cilia are normally set into activity and their rate of beating is modified either by the contraction of underlying muscle fibers or by direct nervous impulses. The fact that cilia continue beating in a magnesium sulphate solution after muscle activity has disappeared shows too that they have the power like ordinary cilia of maintaining movement in the absence of extra-epithelial stimulation, and finally, since their movement persists until they become exhausted or the epithelium breaks down, it is evident that they depend on some extrinsic factor to bring them to rest. In this connection it should be recalled that a foot which has been in sea water for a long time, perhaps for twenty-four hours, shows the cilia everywhere moving at uniform speed over a given area in the complete absence of muscular movement. In the latter case all the cilia were stimulated to movement before nervous impulses and muscular contractility gradually disappeared, and their behavior is the same as it is after these activities are suddenly inhibited by magnesium sulphate. When a foot which exhibits no muscular contractions is placed in a ten per cent. solution of magnesium sulphate the most marked change noted is but a slight retardation in the rate of ciliary movement. A more concentrated solution may bring about a decided slowing down or even a cessation of ciliary action. This appears to be a direct effect upon the ciliated cells, which show normal activity again after the foot has been transferred to sea water.

During the course of one experiment I was surprised to note certain cilia beating in the magnesium sulphate solution which were quiescent after the foot was placed in the solution twenty-four hours previously. An examination of the foot showed that it had revived during its long immersion in the fluid, and that contractions, such as ordinarily accompany the movement of the cilia, were in progress. Another instance of the reoccurrence of muscular and ciliary activity was recorded in the case of a foot which had remained in a magnesium sulphate solution over twenty hours.

A few experiments were carried on in which the snail itself was placed in a solution of magnesium sulphate. The behavior of the cilia was essentially the same as it was when the foot was severed from the more dorsal parts of the body.

Although the ciliary activities on the excised foot of the mud snail were not studied so thoroughly as in the case of *Alectrion trivittata*, enough work was done to convince me that the ciliary mechanism of both species operates in the same way.

Finally a careful investigation was made of the relation between muscular and ciliary movements when the snail was fastened to a support with its foot expanded at the surface of the water. Here also the cilia along the anterior border were seen to start beating as muscle contractions occurred, and to decrease their rate of movement as the contractions subsided and stopped. The lateral foot processes were sometimes swung about and this movement was also accompanied by local ciliary activity. When the cilia were beating actively and continuously the anterior border of the foot showed a vibratory motion caused by a series of rapid contractions and expansions. In addition to the more local muscular contractions correlated with ciliary action, there sometimes occurred irregular foot movements of greater distribution which were unassociated with beating cilia. Movements of the latter type were also observed occasionally when the foot was removed from the body.

CONCLUSIONS.

The observations and experiments briefly recorded above lead me to believe that locomotion in *Alectrion* is the direct result of ciliary action and not arhythmic muscular movements, and the unusual behavior of the cilia points to the conclusion that they have been brought in one way or another under the control of the nervous system. The fact that a resting snail can be made to move its pedal cilia by stimulating the receptors on one of its tentacles with fish meat is in itself sufficient evidence of the controlling action of the nervous system. The muscular movements, which occur when cilia begin beating and which accompany vigorous ciliary activity, may be explained by assuming that efferent impulses arrive at the ciliated cells and muscles at

approximately the same time. It is possible, however, that nervous impulses travel only to the muscles, and that the latter in some way exert a stimulating influence on the overlying ciliated epithelium. Further investigation, both histological and physiological, is planned which, it is hoped, will throw more light on the problem.

LITERATURE CITED.

Crozier, W. J.

- '19 On the Use of the Foot in some Mollusks. Jour. Exp. Zoöl., Vol. 27, pp. 359-366.

Dimon, A. C.

- '05 The Mud Snail: *Nassa obsoleta*. Cold Spring Harbor Monographs, No. 5, pp. 1-48.

Olmsted, J. M. D.

- '17 Notes on the Locomotion of Certain Bermudian Mollusks. Jour. Exp. Zoöl., Vol. 24, pp. 223-236.

Parker, G. H.

- '11 The Mechanism of Locomotion in Gastropods. Jour. Morph., Vol. 22, pp. 155-170.

Walter, H. E.

- '06 The Behavior of the Pond Snail *Lymnaeus elodes* Say. Cold Spring Harbor Monographs, No. 6, pp. 1-35.